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MORPHOLOGICAL VARIATION AND ALLOMETRY OF THE BACULUM IN STOATS, *MUSTELA ERMINEA* (CARNIVORA, MUSTELIDAE) FROM WESTERN CARPATHIANS

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In this study we investigated allometry and variation in the baculum of the stoat *Mustela erminea* and compared it with head-and-body length not involved in reproduction. The stoat is a species with pre-copulatory selection (manifested by the high degree of male-biased sexual size dimorphism) therefore we predicted that baculum allometry may be isometric or exhibited negative allometry. We also test the hypothesis that the baculum size is positively correlated with adult body size and may be used as a reliable indicator of male good condition. Results presented in this study were different according to which regression model type was used. While the OLS slope for baculum length in *M. erminea* indicated negative allometry, the RMA model showed positive allometry. The results obtained for *M. erminea* weren't in agreement with mentioned hypothesis that if baculum allometry is affected by the degree of pre-copulatory selection relative to post-copulatory selection, then we predict isometry or negative allometry of the baculum. Nevertheless, we suggest, that to confirm the above statements further analysis of more numerous material of *M. erminea* coupled with comparative analysis of testicular growth studies are needed to fully understand the importance and function of the baculum relative to the mating system.

Keywords: variability, allometry, *Mustela erminea,* os penis, museum collection.

INTRODUCTION

The baculum is a heterotopic bone in the penis that occurs in males of all species of Carnivora, including the Mustelidae (Abramov 2002, Baryshnikov *et al.* 2003, Miller & Nagorsen 2008, Malecha *et al.* 2009, Krawczyk *et al.* 2011, Schulte-Hostedde *et al.* 2011, Vercillo & Ragni 2011). Morphology of the mustelid baculum has been described in several studies (Burt 1960, van Soest & van Bree 1970, King & Moody 1982, Grue & King 1984, Baryshnikov & Abramov 1997, 1998, Abramov & Baryshnikov 2000, Baryshnikov *et al.* 2003, Elsasser & Parker 2008, Ruette *et al.* 2015, Čanády & Onderková 2016*a, b*), which show that this bone tends to be rather simple in structure but with some more complex projections at the tip. A multi-male mating system occurs in many species of Mustelidae (Lariviére & Jennings 2009), so the baculum may be under strong sexual selection. If so, there may be a limit to baculum growth (Miller *et al.* 1998, 1999, 2000, Oosthuizen & Miller 2000, Miller & Burton 2001, Miller & Nagorsen 2008, Kinahan *et al.* 2008).

Several authors (Dixon 1995, Miller & Burton 2001, Miller & Nagorsen 2008, Demuth *et al.* 2009) showed that females of many mammalian species select mates in part during intromission and evaluate attributes of the penis that are informative about a male's size or other characteristics. Accordingly, if females can benefit by mating with large males and can estimate size of males by size of penis, then positive allometry of penile size relative to body size and small residuals in allometric regression may evolve. Sexually selected traits often show positive allometry and exhibit high phenotypic variation as a result of directional sexual selection (Lüpold *et al.* 2004). Demuth *et al.* (2009) and Krawczyk *et al.* (2011) confirmed that the males in better condition have bigger bacula which confirms that this bone is potentially a good indicator of viability and quality in males. On the other hand, reproductive behaviour and mating system are very important for the evolution of penis size (Miller *et al.* 1998, 1999, 2000, Oosthuizen & Miller 2000, Miller & Burton 2001, Ferguson & Lariviére 2004, Ramm 2007). In contrast, according to Kinahan *et al.* (2008) and Schulte-Hostedde *et al.* (2011), baculum allometry may be isometric or exhibit negative allometry in species with pre-copulatory selection.

Morphological variability of the baculum in the stoat, *Mustela erminea*, has not been investigated. We studied a sample from the Western Carpathians. Our study contributes to the knowledge of quantitative characteristics of bacular size and variation. We also investigated the allometry in the baculum in relation to head-and-body length. Stoats exhibit substantial sexual-size dimorphism, with males being larger than females (Lariviére & Jennings 2009). Therefore if bacula allometry is affected by the degree of pre-copulatory selection relative to post-copulatory selection, then we predict isometry or negative allometry of bacular size.

MATERIAL AND METHODS

Bacula used in this study are in the collection of the Department of Natural History of Šariš Museum, Bardejov. All specimens were collected by T. Weisz, a former curator of museum, as well all individuals were hunting from several localities near the town of Bardejov, i.e., from one small area in north-eastern Slovakia, (49°17′N, 21°17′E, Slovak Carpathians) in the years 1959–1969. Additional information was obtained from the catalogue and protocol cards associated with the specimens (see Hromada *et al.* 2015). Small penis bones (from young) individuals and damaged specimens; damage during preparation or storage were excluded and only data obtained from adult males were used for evaluation (n = 23). Specimens were assigned to the age class adult based on baculum weight (i.e. exceeding 0.03 g) and baculum protuberance (i.e. the presence of protuberance in adult individuals) (van Soest & van Bree 1970, King & Moody 1982, Grue & King 1984, Elsasser & Parker 2008).

Bacular length was measured to ±0.01 mm with a digital calliper, and mass was weighed with a digital balance to ±0.01 g. All bacula were measured according to Čanády 2013, Čanády and Čomor 2013, 2015, Čanády and Onderková 2016*a*, *b*. The measurements

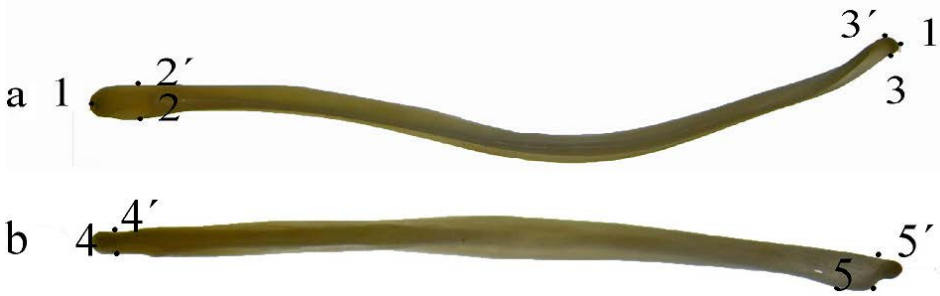

Fig. 1. Baculum measures of *Mustela erminea* used in the study. Lateral (a), dorsal (b) views. All abbreviations of measures: LeBa (1–1′), DvThp (2–2′), DvThd (3–3′), LtLtThp (4–4′), LtLtThd (5–5′) are explained in Material and methods

collected are described in Figure 1a–b and they include: LeBa – baculum length (1–1′), DvThp – dorsoventral thickness of proximal end (2–2′), DvThd – dorsoventral thickness of distal end (3–3′), LtLtThp – laterolateral thickness of proximal end (4–4′), LtLtThd – laterolateral thickness of distal end (5–5′) and finally the WeBa – baculum weight.

The obtained dataset (untransformed data) was evaluated using the following statistical parameters: minimum and maximum (min–max), mean (M), standard deviation (SD), standard error of the mean (SE) and coefficient of variation (CV). Normal distribution was tested by the three normality tests (the Kolmogorov-Smirnov test, the D'Agostino-Pearson omnibus K^2 test and the Shapiro-Wilk *W*-test). Morphometric variation was examined by means of multivariate method (Principal component analysis – PCA). Correlations between the baculum measurements and head-and-body length were analysed using the Pearson correlation coefficient (r_p). Moreover, multiple significance tests with using Bonferroni's correction were performed on correlations among bacular variables in order to the critical $p<0.05$ can be adjusted to $p < 0.001$. Before allometry analysis, measurements were $\log_{10}$ transformed to reduce intra-sample variation and to improve normality. We investigated allometric (log-log) relationships in two steps (Schulte-Hostedde *et al.* 2011). First, ordinary least squares regression (OLS) was used to determine whether slopes differed from zero. If slopes were significant, we proceeded by using reduced major axis regression (RMA) to test for deviations from isometry.

All analyses were performed using MS Excel 2003 for Windows XP and the statistical analysis system GraphPad Prism, version 5.01 (GraphPad Software, Inc., San Diego, California, USA). Ordinary least square (OLS) regression and reduced axis major (RMA) regressions were evaluated by using the program PAST version 2.17b (Hammer *et al.* 2001).

RESULTS

The results of descriptive statistics of the studied baculum variables are presented in Table 1. Result confirmed that the baculum weight together with the proximal parts of bacula were more variables (CV > 25%) in part because of low measurement accuracy, while the baculum length (CV = 5.1%) and distal parts were the less variable (CV < 15%).

The analyses presented in this study showed a strong correlation of the bacular variables between each other and bacular variables between the head-

Table 1. Descriptive statistics of head-and-body length (HBL) and six baculum traits of stoats, *Mustela erminea*. Legend: N – number; min–max – range margins; M – mean; SD – standard deviation; SE – standard error of the mean, CV – coefficient of variance. All abbreviations of baculum measures are explained in Material and methods. Data are given in mm.

Measured traits	N	min–max	M±SD	SE	CV
HBL	21	262.00–289.00	276.3±8.06	1.76	2.9
LeBa	23	22.83–27.12	25.23±1.30	0.27	5.1
DvThp	23	0.84–2.47	1.76±0.52	0.11	29.5
LtLtThp	23	0.64–2.05	1.31±0.38	0.08	29.0
DvThd	23	1.09–1.94	1.44±0.21	0.04	14.4
LtLtThd	23	0.95–1.40	1.16±0.12	0.02	10.0
WeBa	23	0.03–0.07	0.04±0.01	0.00	27.7

and-body length (Table 2), but mainly for the baculum weight (WeBa) with bacular length (LeBa), dorsoventral (DvThp) and laterolateral (LtLtThp) thickness in proximal part. Similar, strong correlation was between baculum length and proximal parts of the baculum. Moreover, all of them were still strongly significant ($p < 0.01$ and/or $p < 0.001$) after Bonferroni correction for multiple comparisons.

The results of PCA showed that the first two principal components (PC1–PC2) explain 87.3% of the variation. The first principal component (PC1) explained 76.6% of the total variance and was correlated mainly with dorsoventral thickness of proximal end (DvThp, r = 0.67), laterolateral thickness of proximal end (LtLtThp, r = 0.62) and baculum weight (WeBa r = 0.40). The second factor (PC2) accounted for only 10.7% and was positive correlated with baculum weight (WeBa, r = 0.90) and negatively with laterolateral thickness of proximal end (LtLtThp, r = –0.33).

Summary results for our OLS and RMA analyses are shown in (Table 3, Fig. 2) and were depending on the regression model used. OLS regression

Table 2. Summary of Pearson's correlations (r_s) between bacular and head-and-body length for a collection of stoats, *Mustela erminea* in Slovakia. All abbreviations of baculum measures are explained in Material and methods. The correlations are shown with the significant levels $^{*}p < 0.05$ and $^{***}p < 0.001$ are signed.

	LeBa	DvThp	LtLtThp	DvThd	LtLtThd	WeBa
DvThp	0.49*					
LtLtThp	0.47*	0.93***				
DvThd	0.05	0.00	0.09			
LtLtThd	0.12	0.20	0.17	0.45		
WeBa	0.59***	0.63***	0.65***	0.10	0.04	
HBL	0.52*	0.23	0.05	0.06	0.25	0.22

Table 3. Results of the OLS and RMA regression slopes, intercepts and 95% confidence intervals (CI), F and p-values for relationships between traits are shown. Explanations of abbreviations of baculum measures see in Material and methods. Significant relationships are shown with the significant levels: NS – statistically non-significant ($p > 0.05$), *$p < 0.05$.

Log Y versus log X variable	N	R^2	OLS slope (95% CI)	Intercept (95% CI)	F	p-values	RMA slope (95% CI)	Intercept (95% CI)	Allometry
LeBa vs HBL	21	0.268	0.848 (–0.669, 0.322)	–0.669 (–2.312, 0.974)	6.961	0.016*	1.638 (0.986, 2.076)	–2.597 (–3.664, –1.003)	positive
DvThp vs HBL	21	0.054	2.762 (–2.804, 8.328)	–6.527 (–20.12, 7.060)	1.079	0.312^{NS}			
LtLtThp vs HBL	21	0.002	0.522 (–4.805, 8.849)	–1.185 (–14.19, 11.82)	0.042	0.840^{NS}			
DvThd vs HBL	21	0.003	0.287 (–2.201, 2774)	–0.550 (–6.622, 5.523)	0.058	0.812^{NS}			
LtLtThd vs HBL	21	0.062	0.878 (–0.760, 2.515)	–2.083 (–6.080, 1.915)	1.258	0.276^{NS}			
WeBa vs HBL	21	0.048	1.924 (–2.185, 6.034)	–6.121 (–16.15, 3.911)	0.961	0.339^{NS}			

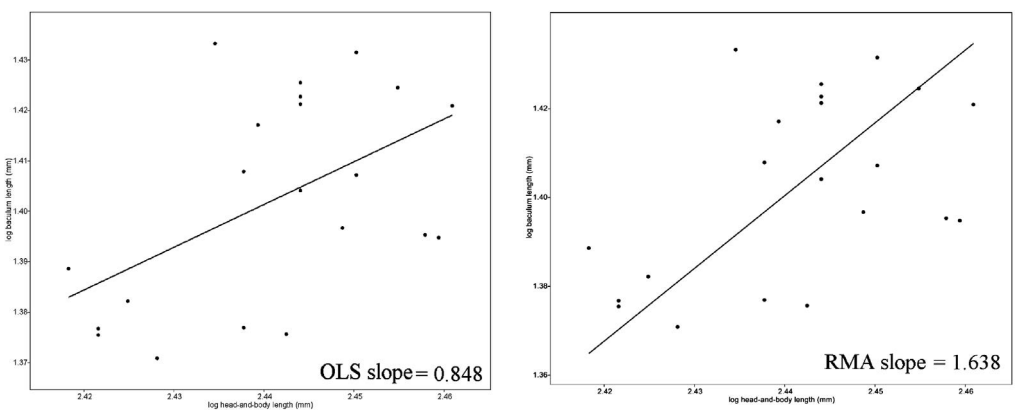

Fig. 2. Relationship between the baculum length (LeBa) in relation to head-and body length (HBL) for a collection of stoats, *Mustela erminea* from Western Carpathians. All variables are log10 transformed. The lines represent the slopes calculated from Ordinary least square (OLS) and reduced axis major (RMA) regressions

indicated and confirmed linear and relatively weak relationship between baculum length and head-and-body length. Result showed that the *M. erminea* baculum exhibited negative allometry, but this was in sharp contrast to RMA slope estimates, which indicated positive allometry for the baculum (Table 3).

DISCUSSION

The baculum grows throughout life (Krawczyk *et al.* 2011) and therefore this growth is connected with the energetic cost and is connected with the risk of infection or breakage. Therefore, baculum may play a role as indicator for a good physical condition of the male (Lariviére & Ferguson 2002). It is very significant, because bacular size is strongly correlated with body size, so could be informative about a male's absolute or relative size during copulation (Miller & Nagorsen 2008). Moreover, several authors (e.g. De Marinis 1995, Miller & Burton 2001, Lüpold *et al.* 2004, Kinahan *et al.* 2008, Krawczyk *et al.* 2011) showed that the largest and heaviest males were favoured by sexual selection as breeders. The bone size served as a reliable indicator of good genes to female mates during breeding (Krawczyk *et al.* 2011). In our previous studies of the baculum in carnivores from Western Carpathians were proved that bacular length was generally less variable than other thickness measurements (Čanády 2013, Čanády & Čomor 2013, 2015, Čanády & Onderková 2016*a, b*). This may be due to the ease of measurement (measurement error), because length measurements are basically error-free. Similar results were obtained for several species of family Mustelidae, i.e. for *Mustela nivalis* (Čanády & Onderková 2016*a*), *Martes foina* (Čanády & Onderková 2016*b*) and *Martes martes* (unpubl. data). Similar analysis in this study confirmed that the bacular length was well correlated with head-and-body length. Positive correlations between the bacular dimensions between each other as well with the baculum weight confirmed their relationship to provide mechanical support during copulation and interact more directly with the female reproductive tract (Baryshnikov *et al.* 2003, Čanády 2013, Čanády & Čomor 2013, 2015, Čanády & Onderková 2016*a, b*).

Reutte *et al.* (2015) proved sexual size dimorphism in favour of males for both species (*Martes martes* and *M. foina*) for somatic measures. For baculum length they showed bigger values for stone marten (*M. foina*) opposite to pine marten (*M. martes*). In species with pre-copulatory selection, the baculum should exhibit isometry or negative allometry together with shallower allometric slopes (Kinahan *et al.* 2008). In contrast, for two species (*Martes americana* and *M. pennanti*) with male-biased sexual size dimorphism was showed different results depending on the regression model used (Schulte-Hostedde *et al.* 2011). These results were not consistent with other studies of mammals

that implicate sexual selection as an important factor in explaining variation in baculum morphology (Miller *et al.* 1999, Miller & Burton 2001, Lüpold *et al.* 2004, Kinahan *et al.* 2007, Tasikas *et al.* 2007, Yurkowski *et al.* 2011). Authors assumed that stabilizing selection rather than sexual selection was the evolutionary force shaping variation in baculum length because allometric slopes were less than one (using the OLS regression model). They assumed that this pattern occurs because post-copulatory selection plays a smaller role than pre-copulatory selection.

Results presented in this study were different according to which regression model type was used. While the OLS slope for baculum length in *M. erminea* indicated negative allometry, the RMA model showed positive allometry. Our results were in accordance with data obtained by Schulte-Hostedde *et al.* (2011) for *Martes americana*. Moreover, our results were different for both species; *Mustela erminea* (showed in this study) and *M. nivalis* (Čanády & Onderková 2016*a*). While RMA slopes indicated positive allometry for *M. erminea*, for *M. nivalis* was confirmed negative allometry. The results obtained for *M. erminea* weren't in agreement with hypothesis that if baculum allometry is affected by the degree of pre-copulatory selection relative to post-copulatory selection, then we predict isometry or negative allometry of the baculum. In contrast, the negative allometry and relative weak relationship between baculum length and head-and-body length in *M. nivalis* are consistent with prediction that the baculum is under stabilizing selection (Schulte-Hostedde *et al.* 2011) for an optimal baculum size. These discrepancies in allometry between both species were similar showed by Schulte-Hostedde *et al.* (2011), for two carnivores of the family Mustelidae, *Martes americana* and *M. pennanti*. Nevertheless, it should be noted, that these differences may be coupled with sample size. The small sample size in *M. erminea* evaluated in this study (n = 23) opposite to bigger size in *M. nivalis* (n = 277).

The present results add new information about morphometric variation in baculum of *Mustela erminea* from Western Carpathians. The results weren't in agreement with hypothesis therefore we suggest, that to confirm the above statements further analysis of more numerous material of *M. erminea* coupled with comparative analysis of testicular growth studies are needed to fully understand the importance and function of the baculum relative to the mating system.

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